AUSTRALIAN LEPTODACTYLID FROGS OF THE *CYCLORANA AUSTRALIS* COMPLEX

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Summary

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Cyclorana australis as now defined is shown to comprise two closely related species: *C. australis* confined to northern Australia and *C. novaehollandiae* to eastern Australia. Notes are provided on the tadpole of *C. australis*, and the calls of both species are analysed. Call divergence is so limited that hybridization is considered possible in sympatry.

Introduction

In recent years, examination of the biology and morphology of several geographically widespread "species" of Australian frogs has revealed that each comprises a complex of species. For example, *Crinia signifera* as recognised by Parker (1940) is now known to be a complex of seven species (Moore 1954; Littlejohn 1957; Main 1957; Straughan & Main 1966; Tyler & Parker 1974); *Mixophyes fasciolatus* is now four species (Straughan 1968) and *Limnodynastes dorsalis* is also four (Martin 1972).

The most neglected leptodactylid genus is *Cyclorana*, of which the type species is *Alytes australis* Gray (1842), described from material collected in the Northern Territory. This species, as currently defined, extends from northern Western Australia to northern New South Wales: a geographic range of approximately 3500 km. The conspecificity of individuals from the extremes of this extensive range is obviously suspect, and even the most cursory comparison of specimens of *C. australis* from the Northern Territory and northern Western Australia with those from Queensland reveals striking differences between them. The northern individuals tend to have a rather elongated head, a distinct, dark rostral stripe and a narrow subocular bar. In contrast, most individuals from Queensland are particularly robust animals with a broad head, and frequently obscure head markings: a population described as *Cyclorana novaehollandiae* by Steindachner (1867), and as *Phractops alutaceus* by Peters (1867). Both names were referred to the synonmy of *australis* by Boulenger (1882).

We have assembled and examined large collections of *C. australis (sensu lato)* from various sources. Here we report our findings and propose the recognition of a complex of two species.

Methods

The specimens reported are deposited in the following institutions: National Museum of Victoria (NMV); Naturhistoriska Riksmuseet, Stockholm (NR); Department of Zoology, University of Melbourne (MUZD); Northern Territory Museum, Alice Springs (NTM); Queensland Museum (QM); South Australian Museum (SAM); and Western Australian Museum (WAM)

Measurements of specimens (to 0.1 mm) were obtained with a pair of Helios dial callipers. Abbreviations employed in the text and tables are as follows: F = foot length (the distance between the proximal end of the tarsus and the distal tip of the fourth toe); HL = head length (the distance between the anterior extremity of the snout and the posterior margin of the tympanic annulus); HW = head width (the maximum width of the head, usually taken at the posterior extremity of the mandibles); TL = tibia length (obtained by placing the tibia between the callipers); S–V = snout to vent length (the distance between

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the anterior tip of the snout and the anterior margin of the cloaca).

Ratios calculated and subjected to the Student t-test were TL/S–V, HL/HW, F/S–V, F/TL and S–V/HW. Larval stage numbers follow those employed by Gosner (1960).

Mating calls were recorded in the field using a Uher 4000 Report portable tape recorder and Beyer M69 dynamic microphone, at a tape speed of 19 cm/sec. Calls were analysed by use of a sound spectrograph (Kay Model 6061–A Sona-Graph) with the overall response curve maintained in the FL-1 position. Three calls of each individual were analysed and mean values calculated. Each call was analysed twice; a narrow-band (45 Hz bandpass) analysis at recording speed to determine duration and dominant frequency, and a wide-band (300 Hz bandpass) analysis at half recording speed to resolve fundamental frequency.

The Cyclorana australis complex

Frogs of the *Cyclorana australis* complex are relatively large animals; the snout to vent length of adult males ranges from 61.4 to 81.4 mm, and that of females from 69.9 to 102 mm. They are all generally robust with a broad and frequently bloated body and relatively short limbs (TL/S–V range = 0.34–0.46). All members of the complex exhibit exostosis of the maxillary, premaxillary, nasal, frontoparietal and squamosal bones. On the dorsolateral body surfaces there are continuous or disrupted, longitudinally orientated skin folds commencing behind the skull, and terminating above the groin.

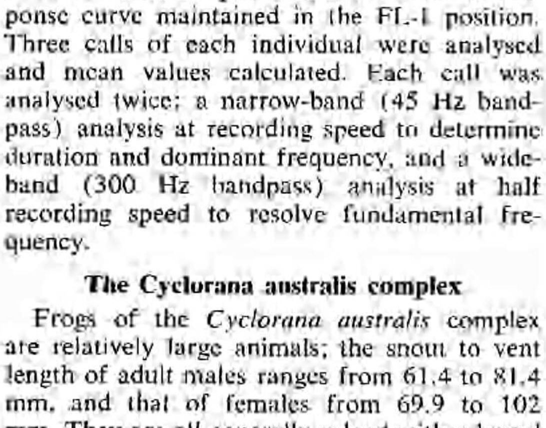

Fig. 1. Geographic distribution of the frogs of the *Cyclorana australis* complex. Circles = *C. australis*; triangles = *C. novaehollandiae*. Closed symbols indicate sites of the material examined, and the open circles one of the following literature references: Brattstrom (1970), Loveridge (1935), Moore (1961), Parker (1940), Slevin (1955).

Nothing is known of the breeding biology of the members of the complex, but they are probably opportunistic breeders. The eggs are small and pigmented (ovidiameters of oviducal eggs range from 1.1 to 1.3 mm), and the tadpole (one species) is of the hylid type with two upper and three lower rows of labial teeth, an acuminate tail tip and a median or slightly dextral anus.

The geographic range of the complex extends from northern Western Australia to northern New South Wales (Fig. 1). Of what we demonstrate to be two component species, *C. australis (sensu stricto)* occurs in northern Western Australia, the Northern Territory and northern Queensland to the west of the Dividing Range; *C. novaehollandiae* is found throughout Queensland and extends as far south as the northern part of New South Wales.

Cyclorana australis (Gray).

FIG. 2A

Alytes australis Gray (1842).

Chiroleptes australis, Gunther (1858); Boulenger (1882) (part).

Phractops australis, Fry (1914).

Cheiroleptes australis, Spencer (1901) (replacement name for *Chiroleptes*)

Cyclorana australis, Parker (1940) (part).

Type locality: "North coast of Australia". (Port Essington, Northern Territory.)

Material examined: Western Australia—WAM, R8732, Carlton Reach, Ord River; WAM, R43067, Crystal Ck; WAM, R1558-59, Drysdale River Mission; WAM, R21233, Fossil Downs; WAM, R1377, 43282-86, 42399-42422, Kalumburu; WAM, R22369-75, Kimberley Research Stn; SAM, R4769-70, R5070, Kununurra; WAM, R1654-57, Landor Stn; WAM, R42387, 80 km S of La Grange; WAM, R42536-40, 42381, 43478, 43491, Mitchell Plateau; WAM, R42530-35, Main Ord River Dam Site (spillway); WAM, R42424, Mt Hart; WAM, R32099, Mt Anderson; WAM, R32291, Mt Barnett; NR, 1562, Mowla Down; WAM, R13726, Oscar Ranges; NMV, D2354-55, Port George IV; WAM, R32149, St George Range. WAM, R11208, R11894, R12332, Woljulum; WAM, R26769-70, Point Springs, Webber Range; WAM, R32351A, Wyndham; WAM, R25093, 40 km SE of Wyndham; WAM, R20307, Yeda Crossing. *Northern Territory*—SAM, R14332, Adelaide River; NMV, D12702, Barrow Ck; NMV, D8307, D8315, D8327, QM, J1785, 2985, SAM,

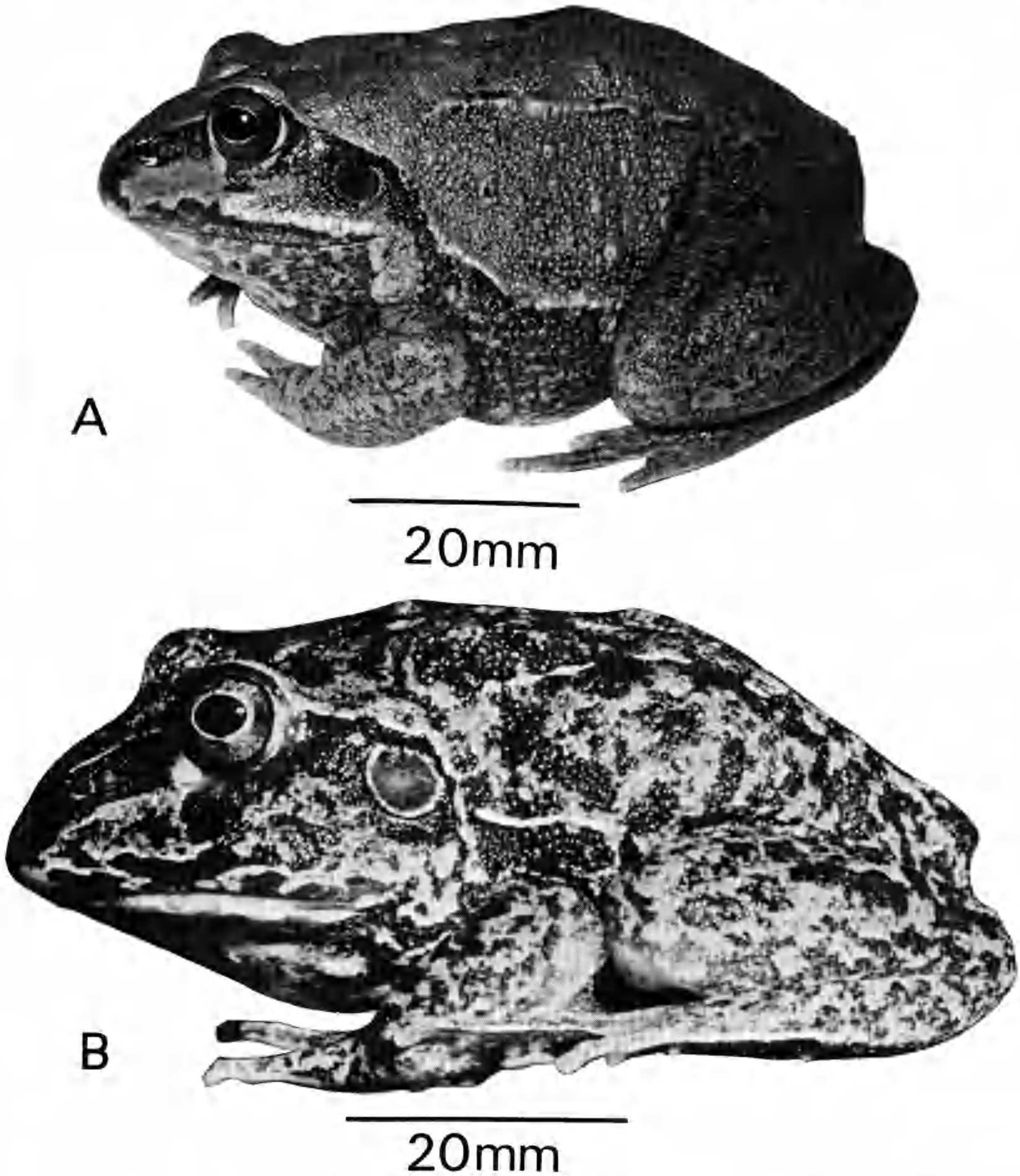

Fig. 2. A. *Cyclorana australis* from Kununurra, W.A. B. *Cyclorana novaehollandiae*, 15 km N of Goondiwindi, Qld.

R8968, Darwin; SAM, R13453, Elsey; SAM, R13450, Howard Springs; WAM, R1935-36, R21318, SAM, R14330-31, Katherine; SAM, R4877, Mt Bundy Stn; SAM, R13349 A-G, Smith Pt, Coburg Peninsula; WAM, R24007, Snake Ck; NMV, D12704-08, SAM, R13275 A-L, Tennant Creek; NTM, 498, 525-26, 50 km N of Tennant Creek. *Queensland*—SAM, R5010, R5070, Doomadgee Stn; NMV, D8437-38, SAM, R4934, Mornington I.

Description: The diagnostic characters of this species are: size large, males 70.8–78.0 mm and females 71.0–81.0 mm in snout to vent length; S–V/HW ratio high (mean 2.31); head width only slightly greater than head length (mean HL/HW ratio 0.89); TL/S–V ratio moderate (mean 0.32); foot relatively long (F/S–V mean 0.40).

Development and exostosis of the superficial skull bones are moderate in this species. The dorsal limit of the squamosal is such that there is a very broad gap between the squamosal and the frontoparietal. On the frontoparietal exostosis is confined to the lateral borders of the bone. The sub-orbital portion of the maxilla slopes steeply to the labial margin and is not expanded there into a lateral ridge.

Cyclorana australis is usually pale olive or grey in preservative and bears a narrow and very sharply demarcated dark brown rostral bar and a narrow sub-ocular bar which terminates far above the labial margin. The lateral body surfaces are commonly heavily suffused with darker pigment. The backs of the thighs are darker and densely variegated with light pigment.

Geographic variation: The presence of darker, irregular patches on the dorsum varies through the range. Dorsal spots are absent from a series of over 100 specimens from Kununurra. Specimens from Tennant Creek have light suffusions of pigment, and those from the north-eastern portion of the range are heavily pigmented with dark stippling. Immaculate and marked specimens occur on Mornington Island.

Variation in some of the pertinent body proportions is summarized in Table 1.

Eggs: A gravid female from Kununurra contained approximately 1000 eggs varying from 1.1 to 1.3 mm in diameter. The eggs have black animal poles.

Larval morphology: A series of tadpoles was obtained at Kununurra on the Ord River by K. Cole in February, 1963. The following notes are based on four specimens from this series at stages 36–39. All specimens are poorly preserved and badly distorted, so that their total length range of 50–65 mm is only an approximation.

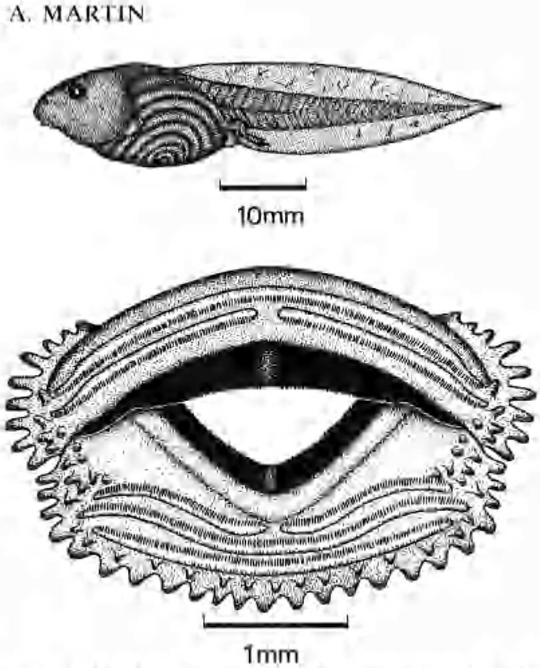

Fig. 3. Tadpole and tadpole mouthparts of *Cyclorana australis*.

The spiracle is sinistral and the anus median or very slightly displaced dextrally. The overall appearance (Fig. 3) is similar to that of *C. cultripes* and *C. platycephalus* (Watson & Martin 1973).

TABLE 1

Geographic variation in proportions of Cyclorana *species*
(Ranges are given with means and standard deviations in parentheses)

Species and locality	*n*	*HL/HW*	*TL/S-V*	*S-V/HW*	*F/TL*	*F/S-V*
C. australis						
Kununurra, W.A.	7	0.81 — 0.93 (0.86 ± 0.04)	0.38 — 0.45 (0.42 ± 0.03)	2.13 — 2.33 (2.23 ± 0.09)	0.91 — 1.00 (0.97 ± 0.03)	0.38 — 0.44 (0.41 ± 0.02)
Smith Point, N.T.	7	0.89 — 0.93 (0.91 ± 0.01)	0.40 — 0.45 (0.43 ± 0.02)	2.27 — 2.44 (2.36 ± 0.06)	0.92 — 0.98 (0.95 ± 0.02)	0.39 — 0.43 (0.41 ± 0.01)
Tennant Creek, N.T.	7	0.87 — 0.94 (0.90 ± 0.02)	0.40 — 0.46 (0.42 ± 0.02)	2.25 — 2.49 (2.36 ± 0.08)	0.91 — 0.98 (0.94 ± 0.02)	0.38 — 0.42 (0.39 ± 0.01)
Mitchell Plateau, W.A.	4	0.95 — 0.99 (0.97 ± 0.01)	0.44 — 0.50 (0.46 ± 0.02)	2.26 — 2.51 (2.41 ± 0.12)	0.88 — 1.05 (0.95 ± 0.07)	0.38 — 0.43 (0.41 ± 0.01)
C. novaehollandiae						
Cooktown, Qld	7	0.81 — 0.83 (0.83 ± 0.02)	0.39 — 0.43 (0.41 ± 0.01)	1.93 — 2.08 (2.02 ± 0.04)	0.87 — 0.96 (0.91 ± 0.03)	0.36 — 0.41 (0.38 ± 0.01)
Calliope, Qld	3	0.82 — 0.88 (0.86 ± 0.03)	0.39 — 0.40 (0.39 ± 0.01)	2.03 — 2.17 (2.12 ± 0.01)	0.89 — 0.94 (0.92 ± 0.02)	0.34 — 0.39 (0.36 ± 0.01)
Cunamulla, Qld	5	0.78 — 0.85 (0.82 ± 0.03)	0.34 — 0.41 (0.37 ± 0.02)	1.97 — 2.13 (2.05 ± 0.06)	0.93 — 1.02 (0.96 ± 0.03)	0.32 — 0.39 (0.36 ± 0.03)

The mouth is subterminal (Fig. 3) with a large horny beak and papillae around the sides and back of the mouth disc. There are two upper rows of labial teeth, the second disrupted medially, and three lower labial rows of which the first is similarly disrupted.

Mating Call: Calls of five individuals were recorded on 13.xii.1971, 14 km E of Daly Waters, N.T. The frogs were calling on land beside a small water-filled channel. Wet-bulb air temperature at the calling sites was 24.1°C. The call is a short, well-tuned note repeated in long sequences. The mean call duration is 152 msec (range 122–204). The fundamental frequency is 199 Hz (range 183–209), but contains little energy: most of the energy is in the third, fourth and fifth harmonics (about 600, 800 and 1,000 Hz) which are approximately equally emphasized.

Geographic Range: Cyclorana australis extends from the Kimberley District of northern Western Australia to the Gulf District of Queensland. In the Kimberleys it is clearly widely distributed, and in the Northern Territory it extends as far inland as Barrow Creek. Absence in the north-western portion of the Northern Territory may simply reflect inadequate sampling.

Cyclorana novaehollandiae Steindachner.

Cyclorana novaehollandiae Steindachner (1867).
Phractops alutaceus Peters (1867).
Chiroleptes australis, Boulenger (1882) (part).
Phractops australis, Loveridge (1935).
Cyclorana australis, Parker (1940) (part); Moore (1961), plate 35, Fig. 2.

Type locality: Rockhampton, Qld.

Material examined: Queensland—NMV, D13049, SAM, R9817, R9835, Battle Camp; MUZD, 90-92/70, 5 km SW of Calliope; QM, J431, Colosseum; QM, J18062, J18066, Condamine River, Cecil Plains; NMV, D13049, SAM, R11523-24, Cooktown; QM, J20685-91, 8 km W of Cooktown; SAM, R9690, Edward River Stn; QM, J2184-85, J12944, Eidsvold; QM, J14383-84, Gilruth Plains, Cunnamulla; MUZD, 56-58/70, 75/70, 9 & 15 km E of Goondiwindi; QM, J5611-12, Mackay; SAM, R4743, Mapoon Mission Stn; SAM, R9734, Mary River; QM, J14159-67, Mitchell R. Mission; SAM, R10419, Prestwood, Gilbert River; SAM, R3640, Rockhampton; QM, J10482, SAM, R3686, St George; QM, J2186-89, Stannary Hills; SAM, R1935, Stewart River; SAM, R9691, Strathgordon H.S.; QM, J22227-29, Surat; NMV, D7542, QM, J4644, Townsville; QM, J3480, Victo, Coongoola; QM, J18063-65, Waratah Stn, Cunnamulla.

Description: Snout to vent length of males 61.4–81.4 mm, females 74.8–101.2 mm; head noticeably broader than long (HL/HW mean 0.83); S-V/HL ratio low (mean 2.05). TL/S–V ratio rather low (mean 0.40); foot short (F/S–V mean 0.37).

There is extreme exostosis of the skull bones. The squamosal in large specimens is usually so heavily overlain with secondary bone that it is visible through the skin, forming humps resembling parotoid glands, and extends so far superiorly that it approaches the margins of the frontoparietals. The frontoparietal is entirely exostosed, but the lateral margins are raised by bone deposition, so producing a deep, median furrow. The suborbital portion of the maxilla projects, forming a high and often concave shelf.

The constricted pupil in six living specimens from Cooktown approximated a rhomboid shape (see discussion).

In preservative, *C. novaehollandiae* is pale brown or grey, and is immaculate, lightly marked with scattered dark brown or blackish markings, or else very densely pigmented with such markings. The suborbital marking is broad and usually reaches the labial base of the maxilla. The backs of the thighs are usually very dark leaden grey and lack lighter vermiculations.

In life the series from Cooktown were an immaculate dull sandy yellow dorsally. The rostral stripe was dark brown, and similarly colored, small disrupted patches occurred on the inferior margin of the maxilla. The iris was golden and suffused with dark brown laterally and inferiorly. The posterior surfaces of the thighs were leaden grey, whilst the ventral surface of the body wall was a dull pearl bearing faint grey vermiculations on the throat.

Geographic variation: There is considerable variation in skull structure and coloration of the dorsum of this species. Comparison of small samples of extreme variants led us to conclude initially that two species were involved. Examination of larger series, however, has revealed the occurrence of forms of intermediate appearance. The variation may be summarized as follows. All specimens from central and southern Queensland have high skulls with a gently sloping maxilla and a densely pigmented dorsum. There is striking variation in individuals from northern Queensland. Some are densely pigmented whilst others are immaculate. The skull of the immaculate individuals is either similar to that of the pigmented frogs, or is spatulate and distinctly flattened. Unfortunately we have been unable to devise a means of objectively estimating skull depth with any degree of accuracy. We hold the opinion that the high and the spatulate forms of the skull represent different evolutionary trends of development.

Whereas the extremes are clearly different, assessment of the significance of the observed variation is complicated by the existence in northern Queensland of a number of intermediate forms that cannot be referred to either form. In addition there are animals in which the terminal portion of the skull is more elongated. This variant occurs only on the Cape York Peninsula and at localities at the base of the Gulf of Carpentaria. Morphometric data of two small series are summarized in Table 1.

Eggs: Oviducal eggs of three gravid females ranged from 1.1 to 1.3 mm in diameter. An estimate of the number in one individual exceeded 1,000. The eggs have black animal poles.

Mating Call: The mating calls of two individuals recorded 5 km SW of Calliope, Queensland, on 18.i.1970, are very similar to those of *C. australis*. The frogs were calling on land beside a rain-filled roadside ditch, with a wet-bulb air temperature of 24.6°C. The spectral structure of the calls of the two species is essentially identical, with *C. novaehollandiae* also having emphasized harmonic bands at about 600, 800, and 1,000 Hz. However, its call duration is considerably longer (mean 249 msec; range 235–262 msec). Judged on the basis of the levels of difference in mating call structure of sympatric anuran species, this difference in duration does not represent divergence of sufficient magnitude to achieve reproductive isolation. Hence if *C. australis* and *C. novaehollandiae* occur in sympatry (as they may in the Gulf District) we would expect them to hybridize. A similar pattern of marked morphological differentiation, accompanied by very little mating call divergence, characterizes the Western Australian *Limnodynastes dorsalis* and the eastern *L. dumerili* (Martin 1972).

Geographic Range: Cyclorana novaehollandiae ranges from the Cape York Peninsula of northern Queensland to the New South Wales border.

KEY TO ADULTS

Back of thighs variegated, suborbital bar narrow and not reaching base of maxilla; maxilla gently sloping and not expanded laterally ...... *C. australis*

Back of thighs not variegated; suborbital bar (if present) usually broad and reaching base of maxilla; maxilla expanded to form lateral shelf *C. novaehollandiae*

Discussion

The morphological complexity of *C. novaehollandiae* as defined here is unparalleled amongst Australian anurans. We believe that a study of species isolating mechanisms, such as male mating call, in north-eastern Australia could reveal the existence of two or possibly even three species. Our action of resurrecting *C. novaehollandiae* from the synonymy of *C. australis* is therefore only the first step towards an understanding of the *C. australis* complex. The biological data, e.g. mating call structure, that are necessary for final resolution of the problem may be extremely difficult to obtain. The northern Queensland populations are apparently opportunistic breeders which may call at a locality on only one or two nights each year (C. Tanner, pers. comm.). It seems justifiable, therefore, to treat the complex at this preliminary level.

In terms of skull structure, *C. australis* is clearly the most simplified and primitive member of the complex, exhibiting limited development of skull bones and the least extensive exostosis. All the variations in the form of the skull and exostosis of the cranial bones such as the maxillary and squamosal in *C. novaehollandiae* can reasonably be derived from *C. australis*.

The concept of *C. australis* being the primitive member may be acceptable morphologically, but it is more difficult to conceive zoogeographically in view of the absence of any member of the genus *Cyclorana* in New Guinea. The geographic area occupied by the members of the *C. australis* complex includes both high rainfall and relatively arid areas; i.e. it does not appear to be limited climatically. Thus if the complex originated in northern or north-western Australia it is surprising that it should be absent from New Guinea. Jennings (1972) estimates that the most recent land communication with New Guinea at Torres Strait terminated only 6,500–8,000 years ago; thus it is possible that colonization of north-eastern Australia by the complex occurred subsequently.

The gross differences in morphology characterizing the members of the *C. australis* complex represents a situation unique among Australian anurans. Differentiation in other species complexes, even those with extensive disjunctions of range (e.g. south-eastern and south-western Australia) is accompanied by only slight morphological divergence. It seems probable, therefore, that the complex is of considerable antiquity. Two further circumstances lend support to this suggestion. One is the affinity of *Cyclorana* with the Hylidae demonstrated by Tyler (1972) and Watson & Martin (1973). The other stems from our observations on the pupil shape of *C. novaehollandiae*. As stated above, the constricted pupil of *C. novaehollandiae* is almost rhomboid. In fact, the ventral margin is an obtuse angle and the upper a broad curve. This curvature is difficult to detect during extreme constriction. Lynch (1971) considers the vertically orientated pupil to be the primitive and the horizontal pupil the derived state. However, from the fact that *Nyctimystes* (a genus that can only be derived from *Litoria*, a horizontally-pupilled stock) has a vertical pupil, it is clear that vertical orientation can be a derived state. The trend to one or other orientation of pupil shape could be accomplished most readily from a rhomboid. That such a structure occurs in living *Cyclorana* is consistent with our hypothesis of its antiquity.

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